# GRAMINOID RESPONSES TO GRAZING BY LARGE HERBIVORES: ADAPTATIONS, EXAPTATIONS, AND INTERACTING PROCESSES[1]

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## ABSTRACT

The problem of ascribing adaptive significance to traits that enable graminoids to tolerate or evade ungulate herbivory is examined. Some of these traits may have originally evolved in response to non-grazing selection pressures, thus constituting grazing exaptations rather than true adaptations. The fossil record indicates that semiarid habitats, extensive grasslands, and grazers appeared, interacted, and evolved together. However, several traits that are advantageous in semiarid habitats have beneficial effects for grazed plants. Other traits, such as developmental plasticity, enhance competitive ability in certain environments, but also increase grazing tolerance or resistance. Experiments and simulation modeling showed that defoliation responses are embedded in a network of interacting processes, including photosynthesis, transpiration, nutrient uptake, and resource allocation. Responses and adaptations to defoliation must be interpreted in this context. Although traits may have arisen due to non-herbivorous selection pressures, they may subsequently have been selected, combined, or amplified through grass-grazer coevolution to form species, polymorphic populations, phenotypically plastic individuals, or communities of species that evade, resist, or tolerate herbivory.

Graminoid grazing tolerance and the nearly simultaneous increase of grasses and grazers in the fossil record (Stebbins, 1981) suggest that grasses are adapted to herbivory, perhaps as a result of coevolution. Grasses and herbivores may, consequently, be somewhat mutualistic (Owen & Wiegert, 1981). Graminoid tolerance of herbivory due to continued elongation from the base of the leaf and lateral growth through tillering following defoliation have long been known (Lisle, 1757; Arber, 1934). Interacting physiological and morphological characteristics of graminoids that contribute to such grazing tolerance have been identified (McNaughton, 1979a) and analyzed (Coughenour et al., 1984b, 1985a). However, the origin of present traits in organisms cannot always be attributed to selection pressures of their present environment (Gould & Lewontin, 1979). The current beneficial effect of a trait is actually incidental or secondary if the trait frequency increased in response to another previous selection pressure. Thus, we must distinguish between beneficial traits (aptations) that are only incidentally beneficial (exaptations), and traits that have actually resulted from selection pressures to confer their present benefits (adaptations) (Gould & Vrba, 1982). We should con-sider alternative non-adaptive hypotheses in any investigation of the presumed adaptive significance of traits (Eriksson et al., 1983).

Evolutionary constraints reduce the variety of evolutionary options available to a species. A trait may be non-adaptive in the sense that it is a necessary consequence of another trait (Eriksson et al., 1983). More fundamentally, individual traits are not in themselves the targets of natural selection. It is the fitness of the whole organism, or interacting system of traits, that determines the outcome of natural selection (Mayr, 1983). This "cohesion of the genotype" results in inevitable compromises among competing demands and a residue of sub-optimal parts that are necessary for the working of the whole (Mayr, 1983). Most plants are in essence metapopulations (White, 1979) of repeating modular units (Harper, 1981). The effect of herbivory on modular organisms differs from the effect of predation on non-modular organisms in that modular organisms survive predation through vegetative reproduction, whereas non-modular organisms do not. Therefore, it is necessary to consider defense against herbivory in a context of other interacting physiological processes and morphometric traits. Factorial experimentation and simulation mod-

eling are used here to examine interactive processes, causal networks, and possible competing demands that are relevant to herbivory response in perennial graminoids.

## EVOLUTIONARY HISTORY OF GRASSES AND GRAZERS

The original selection pressures that gave graminoids their current morphological and physiological characteristics can never be absolutely known. However, some insight can be gained by examination of the origins of grasses in relation to grazers in evolutionary time and space. These origins must be related as well to pre-grazing ancestors to determine possible preadaptiveness of traits, and to non-grazing selection pressures such as climate, which may have given rise to grazing exaptations.

Monocotyledons as a broad group are evolutionarily more advanced than dicotyledons, exhibiting neotony as an evolutionary response to extreme environmental conditions, particularly to an aquatic habitat (Takhtajan, 1969). Linear, parallel-veined leaves that grow from their bases arose from modified bladeless petioles, and the sheathing bases of monocot leaves are a consequence of the single cotyledonary structure (Cronquist, 1968). The first monocotyledons probably arose in the Cretaceous period (135–70 Ma) (Raven & Axelrod, 1974).

By the tertiary period (70 Ma) most ancestral grasses had differentiated. Predominantly xerophytic types developed to the south into Africa (Jacques-Felix, 1962). However, there are basically three contrasting theories (Whyte, 1974) regarding the origin of primitive grasses: (1) origin in the humid tropical forests, with increasing evolutionary advancement correlated with greater adaptation to aridity (Bews, 1929); (2) origin in open forest followed by migration into xerophytic zones (Valentine, 1970); (3) origins in mesophytic and xerophytic zones with subsequent mixing of types (Aubreville, 1962; Thomas, 1966). A typical primitive grass may have been a small, low-growing perennial, somewhat tufted, with short leaves, and probably forest-loving (Stebbins, 1972).

Early grasses and hypsodont-toothed mammals first appeared in the fossil record in early Eocene (60 Ma) strata of South America. During the Oligocene (40–25 Ma) several new groups of notungulates appeared in the first open savannahs in South America. In the Miocene (25–12 Ma) horses with more refined hyposodont teeth appeared, and predominated the large herbivore fauna of North America (Stebbins, 1981). Semiarid conditions appeared in South America 20 million years earlier than in North America, but the greater continentality of the North American climate caused more rapid changes in environmental selection pressures (Stebbins, 1981). The Rocky Mountain uplift, and resulting aridity of the Great Plains caused a retreat of forests in late Oligocene and Miocene (30–12 Ma) leaving drought-tolerant grasses and herbs behind (Dix, 1964). Close-grazing bison and sheep arrived in North America from Eurasia in the Pleistocene (3–0.01 Ma) (Mack & Thompson, 1982; Stebbins, 1981). Equidae and Camelidae migrated from North to South America at the end of the Pliocene (3 Ma) or early Pleistocene (Stebbins, 1981).

Existence of grass savannahs in Africa beginning in the Eocene (60–40 Ma) is suggested by the sparse fossil record of this period (van der Hammen, 1983). Poaceous grasses may have entered South America from Africa during the Paleocene (70–60 Ma) or even uppermost Cretaceous (Stebbins, 1981).

In Africa, the Eocene-Miocene (60–12 Ma) was dominated by perissodactyls and proboscideans. Increasing continental elevation was accompanied by increased aridity in the Oligocene (40–25 Ma) (Raven & Axelrod, 1974). Grazing, ruminating bovids appeared first in fossils of the late Miocene (18–12 Ma) in Eurasia and radiated greatly during the Pliocene (12–3 Ma), but they did not invade Africa until late Pliocene (Sinclair, 1983). In the late Pliocene-Pleistocene (4–0.01 Ma) the climate fluctuated in Africa, causing fluctuations in vegetation types and expansion-contraction cycles of savanna habitats. As a result, there was great adaptive radiation in the African large herbivore fauna (Morton, 1972). There may have been significant evolutionary development of grass species at this time (Love, 1972).

Thus, grasses evolved at an early date and existed for quite some time prior to abundant grazing animals. Increasing specialization and adaptations to aridity occurred among grasses subsequently. Extensive grasslands, grazers, and semiarid climates appeared almost simultaneously. This simultaneity makes it difficult to ascertain the original adaptive values of traits that enhance survival under both aridity and grazing.

## ADAPTATIONS FOR DROUGHT OR GRAZING?

A number of traits that allow graminoids to evade, resist, or tolerate drought provide similar benefits to plants subjected to grazing. These traits are basal meristems, small stature, high shoot density, deciduous shoots, belowground nutrient reserves, and rapid transpiration and growth.

Linear leaf elongation from an intercalary meristem at the base of the leaf is an ancient trait of monocotyledons. This trait probably made it more feasible for some monocots to maintain intercalary meristems in a protected position at the base of the plant during vegetative growth. Basal meristems, protected by the basal sheath in grasses, may be better able to withstand drought (Barlow et al., 1980). Many perennial grasses have reduced bud height, which is regarded as a means to survive a stressful non-growing season (Raunkaier, 1934). However, primitive grasses adapted to semiarid habitats "probably had already developed enough of a basal intercalary meristem to enable leaves to recover from grazing" (Stebbins, 1972).

Small stature is a well known characteristic of many graminoids that are adapted to more arid habitats. Water and time both impose an upper limit on individual shoot size. In general, however, there is an inverse relationship between shoot size and shoot number (Gorham, 1979). Having many small shoots facilitates rapid response to ephemeral water availability, distributes the risk of drought-induced mortality, and increases the rate of recovery from defoliation. A shorter growth form is also less likely to have a large proportion of its leaves removed by large herbivores.

Deciduous shoots allow perennial graminoids to survive drought by reduction of both transpiring leaf area and shoot maintenance respiration. However, senescent leaves are low quality food items that limit herbivore population sizes (Sinclair, 1975) and, therefore, herbivore impacts. Drought-deciduous leaves are relatively inexpensive to construct compared with leaves of drought-enduring plants (Orians & Solbrig, 1977; Mooney & Gulmon, 1982), and therefore herbivore damage is less costly to the plant. Exportation of nutrients back to perenniating organs during senescence (Williams, 1955) further reduces the impact of herbivory (Mattson, 1980).

Perennial grasses endure the dry season with carbon and nutrient reserves stored in sub-surface crowns and roots. When moisture returns, regrowth proceeds at a rate in excess of current photosynthesis, dependent on upward translocation from reserves. This adaptation to a non-growing season is critical for regrowth following defoliation (Trlica, 1977).

Drought-deciduous perennials that are active only in a wet season should be under strong selection pressure to evolve morphological and physiological traits to maximize production when water becomes available (Orians & Solbrig, 1977). Whereas drought-tolerant shrubs use water slowly when wet and continue to transpire when dry, grasses use water rapidly when wet and cease transpiration when dry. Rapid transpiration implies rapid photosynthesis and growth, which help plants recover from defoliation.

## ADAPTATIONS FOR COMPETITION OR GRAZING?

In a competitive environment it is adaptive for a plant to have higher plasticity of root–shoot allocation to enable rapid exploitation of light, or soil water, or nutrient resources, as they become available (Grime, 1977). Rapid shoot regrowth and associated diversion of photosynthate from roots to shoots enables rapid response to changing resource availability. For example, a sudden reduction of leaf area causes a shift from water to light limitation, thus requiring rapid diversion of resources to shoots.

The most primitive grasses were small, and the most general trend in grass evolution has been to increase in size, through increased activity of intercalary meristems (Stebbins, 1972). Through sequential activation of the meristems of stem internodes, the meristems of leaf blades are elevated on culmed shoots. This provides a more effective display of leaf area than does a basal origin of all leaf blades, thereby increasing light competitive ability. Increasing lignification and canopy heights associated with graminoid stem growth reduces or deters herbivory (Stobbs, 1973; Jarman & Sinclair, 1979; van Soest, 1982).

The bunchgrass growth form has been hypothesized to be inherently less resistant to herbivory than more rhizomatous or stoloniferous growth forms, possibly due to coevolution of the latter with large herbivores (Mack & Thompson, 1982). However, the way plant modules are arranged relative to one another may have adaptive significance distinct from herbivory tolerance. Vegetative reproduction by tillering is an efficient method of colonizing open sites. Exten-

sive asexual reproduction also decreases the probability of genotypic extinction (Cook, 1979). A plant with short horizontal internodes and tillers packed in a bunch or tussock grows as an advancing front or "phalanx," forming an impenetrable zone of resource preemption. Plants with vigorous horizontal spreading or tillering, on the other hand, have the "guerilla-like" tactic of spreading over an unoccupied area quickly (Harper, 1981). The guerilla growth form is adaptive for plants that compete for space in early successional stages or disturbance sites. Once established, however, protection against invaders is more advantageous. The guerilla-phalanx dichotomy involves a trade-off of resource investment inherent in lateral versus horizontal growth.

Several other traits may allow rapid colonization of open space and increased competitive ability in early successional environments (Bazazz, 1979). These include rapid growth rate, non-light-saturated photosynthetic rate, rapid transpiration and photosynthesis, and reduced sensitivity to decreased water availability. These traits may enable better recovery from defoliation as well.

## DEFENSIVE CHEMISTRY—DOES IT, SHOULD IT, OR CAN IT OCCUR IN GRASSES?

Lignin and silica both reduce palatability; however, it is likely that their primary functions in grasses are non-defensive. Silica reduces digestibility in some grasses, increases it in others, invariably wears down herbivore teeth, and can cause kidney stones (van Soest, 1982). Silica concentrations are sometimes higher in more heavily grazed plants, genotypes or species (McNaughton & Tarrants, 1983; Brizuela, 1985), but this might be taken as evidence either for or against defensive utility. Defoliation induces elevated silica levels in individual plants of some grasses (McNaughton & Tarrants, 1983) but not of others (Cid, 1985). Although invertebrate herbivory is deterred by silica, deterrence of ruminant herbivory has not been demonstrated. Lignin is indigestible, and it can reduce the digestibility of associated carbohydrates (van Soest, 1982). However, both silica and lignin impart rigidity to the cell wall and prevent wilting when cell water contents decrease, as during mild droughts. Xerophytic plants generally have thicker cell walls and are more lignified (Sinnott,

1960). Lignin (Higuchi, 1981) and silica (Russel, 1973) enable terrestrial plants to develop upright forms and be resistant to environmental stress and disease. Thus, grasses that grew in drier, more open habitats evolved firmer and more silaceous leaves, which probably prompted the evolution of hypsodont dentition among grazers (Stebbins, 1981).

Non-lignin phenolic compounds could affect ruminant herbivory of grasses. Tannins and flavones have been isolated from East African grasses (Field, 1976); nevertheless, these species are important forage for native ruminants. Terpenoids occur in another African grass, *Cymbopogon excavatus* (Field, 1976). Regrowth is grazed but mature plants are avoided. Flavonoids and coumarins also occur (Wong, 1973). These compounds have not been shown to deter ruminant grazing.

Grasses lack the variety of toxic chemicals that deter herbivory in dicotyledons. Alkaloids have been isolated from only 21 grasses out of 8,000 examined (Culvenor, 1973). The only alkaloid-bearing grasses that have been shown to affect ruminants, however, are *Phalaris tuberosa, Lolium perenne* (Culvenor, 1973), and *Festuca arundinacea* (Bush et al., 1970). Cyanogenic compounds were detected in only two of 16 grasses (Gibbs, 1974); however, these have not been shown to affect ruminants.

Ruminal microflora are able to degrade a number of otherwise defensive compounds before they reach the stomach. It has been hypothesized that pregastric fermentation originally evolved because it could detoxify secondary compounds in browse plants (van Soest, 1982). Although some tropical grasses contain oxalates that inhibit nutrient absorption by the non-ruminant digestive system of horses (Blaney et al., 1981), the microflora of ruminants degrade the oxalate before it reaches the stomach (Allison et al., 1977). Rumen microflora of domestic sheep have been shown to detoxify alkaloids (Dick et al., 1963) and toxic isoflavones (Nilsson et al., 1967). Several wild ruminants commonly feed on the poisonous fruit of the East African herb *Solanum incanum* L. (Pratt & Gwynne, 1977).

Thus, some chemical constituents do, and therefore can, defend grasses from herbivory, at least to some extent. However, the effectiveness of chemical defenses is limited by the ability of rumen microflora to degrade them. Although lignin and silica have non-defensive functions, they may reduce palatability enough to decrease se-

TABLE 1. Summary of clipping effects on growth and photosynthesis of a short sedge, a mid-grass, and a tall-grass subjected to factorial variations in clipping height (cm) and frequency (d). Compared to unclipped controls, there were stimulations (+), inhibitions (−), and no differences (0).

|  | K. nervosa | T. triandra | H. filipendula |
|---|---|---|---|
| Height of plant | 10–25 | 50–120 | 100–150 |
| Clipping regimes | 2, 5 cm/2, 7 d | 3, 6 cm/3, 7 d | 10, 15 cm/7, 14 d |
| Aboveground growth |  |  |  |
| Total | + | − | − |
| Tillering | − +[d] | 0 | 0 −[a] |
| Leaf elongation rate[b] | + | + | + |
| Residual leaf area | − +[d] | − | − |
| Belowground growth |  |  |  |
| Root growth | −0[c] | − | 0 |
| Crown growth | − +[d] | − | 0 |
| Photosynthetic rate | + −[e] | − +[f] | + |
| Stomatal conductance | + −[e] | 0 | + |
| Internal conductance | 0 | − +[f] | + |
| Water status | +[g] | 0 | +[h] |

[a] Inhibited in 14 d, no effect in 7 d clipping treatments.
[b] Short-duration measurement mid-way through experiment.
[c] Inhibited in 2 d, 2 cm treatments.
[d] Inhibited in 2 cm, stimulated in 5 cm treatments.
[e] Stimulated in 2 cm, inhibited in 5 cm treatments.
[f] Inhibited in 3 d, stimulated in 7 d treatments.
[g] Soil water conservation.
[h] Plant water conservation.

lection pressure for other defensive compounds. The benefits of chemical defenses are further reduced by other, morphological or physiological, traits that enable deterrence, tolerance, or evasion of herbivory.

INTERACTIVE PROCESSES AND MORPHOMETRIC TRAITS IN THREE SERENGETI GRAMINOIDS

The responses of grasses to defoliation are imbedded in and determined by a network of interactive physiological processes and morphometric traits (McNaughton et al., 1982). Intensive laboratory experiments with three Serengeti graminoids (McNaughton et al., 1983; Wallace et al., 1984; Coughenour et al., 1985a, 1985b) elucidated this causal network. The short-, mid-, and tall-statured species represented a range of habitat aridity in the Serengeti ecosystem of northern Tanzania.

Qualitatively different responses to defoliation were exhibited by the three species (Table 1). Total aboveground growth, residual leaf area, and tillering were stimulated by clipping only in the short-statured species. However, leaf elongation rate was enhanced in all three species. In turn,

clipped yield was significantly correlated with leaf elongation rate in all species. Positive photosynthetic responses to defoliation, mediated by stomatal and internal leaf conductances, compensated for reduced leaf area consistently in the tall-statured species and variably in the short- and mid-statured species. This prevented negative belowground growth responses in the tallest species. Belowground growth was correlated with residual leaf area and tiller number in all species. In general, the tallest species had the most homeostatic response, but the underlying adjustments were the most complex.

Water status of the short and tall graminoids was improved by defoliation. Water additions affected growth in both species and photosynthesis of the latter, suggesting that responses to defoliation were partially mediated by water.

Variations in habitat aridity and light competition exert differential selection pressures upon plant growth form that subsequently influence defoliation responses. The inherent tendencies of shorter-statured species to allocate shoot growth in the horizontal direction via tillering, and for taller-statured species to allocate in the vertical direction via leaf elongation, largely influenced
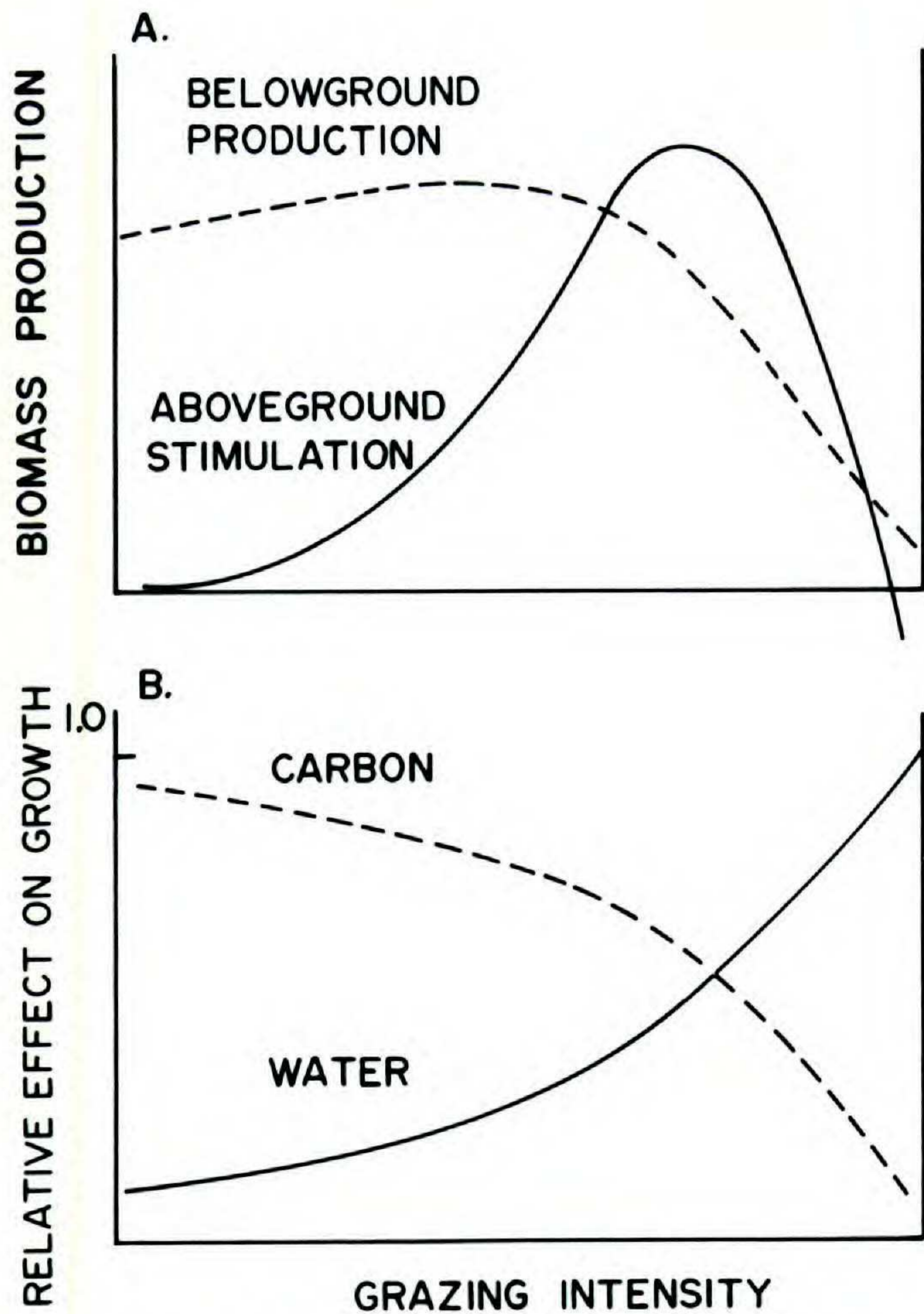
FIGURE 1.—A. The relationship between aboveground biomass stimulation, belowground productivity, and grazing intensity in simulated grasses.—B. The effects of water and carbon on growth, plotted against grazing intensity on the simulated plants. Effects are multiplicative in the model. (Adapted from Coughenour et al., 1985a.)
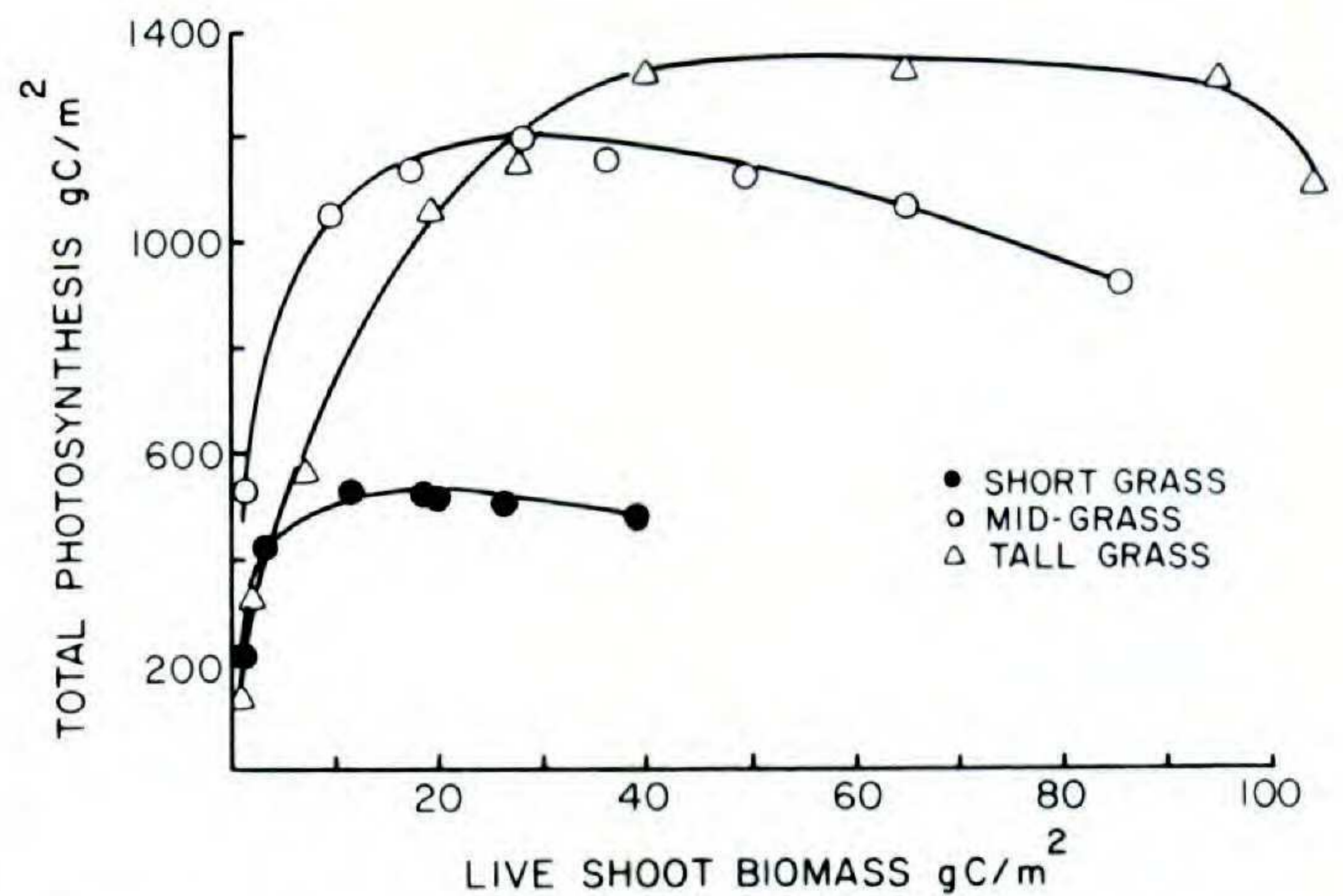


FIGURE 2. Total photosynthesis over a single growing season versus average live shoot biomass of simulated short-, mid-, and tall-grasses. Each point represents a different grazing regime. (Data from Coughenour et al., 1985a.)

nutrients via clipping and nitrogen source (Ruess, 1984).

## MECHANISTIC SIMULATION ANALYSES OF CLIPPING RESPONSES

A simulation model was constructed (Coughenour et al., 1984a) that incorporated morphological and physiological aspects of graminoid growth hypothesized to play a role in plant response to defoliation. The model simulated physiological processes that controlled carbon, water, and nitrogen uptake rates and allocations within the plant. The model simulated meristem types and numbers, tissues types and masses, and canopy geometry. Simulation experiments were performed with short-, mid-, and tall-grasses subjected to various clipping heights and frequencies (Coughenour et al., 1984b; Coughenour, 1984).

Response surfaces of yield to grazers (clipped yield) versus grazing height and frequency indicated that shorter graminoids were optimally defoliated at greater frequencies than taller graminoids, primarily because a large number of small shoots reach their maximum sizes more rapidly than a small number of large shoots. Maximum aboveground productivities were achieved at intermediate grazing intensities (Fig. 1A) when aboveground growth was maximally stimulated. Belowground growth was depressed little at low to moderate grazing intensities but declined rapidly at higher grazing intensities. Greater photosynthetic rates lessened reductions in belowground growth. The aboveground growth response to grazing intensity was unimodal pri-

which of these mechanisms was the more important defoliation response. Similarly, shorter species had inherently greater root/shoot and crown/shoot ratios, that influenced plant responses via the impacts of root biomass on nutrient uptake and crown biomass on nutrient storage and meristem production.

Additional experimentation with *Kyllinga nervosa* has revealed that plant nitrogen relations and grazing responses are highly interactive. Nitrate and ammonium had differential effects on plant responses to clipping, while clipping stimulated uptake rates of both ions (Ruess et al., 1983). Urea nutrition increased material flows to grazers and to plant reproduction, while clipping and urea together resulted in stimulated leaf and flower production, thus establishing a positive feedback from grazers to plants to grazers (Ruess & McNaughton, 1984). Furthermore, grazing affected the balance of several other plant

FIGURE 3. Total belowground productivity versus total photosynthesis of simulated plants for a single growing season. These are the same simulations as in Figure 2.

marily because relative water availability increased while relative carbon availability decreased as grazing intensity increased. Total available photosynthate decreased as more was removed by defoliation, but total transpiration and rainfall interception decreased.

Total photosynthate production was maximal at intermediate levels of live shoot biomass (Fig. 2). The increase in photosynthesis was greatest at low levels of shoot biomass, indicating the critical dependence on leaf area at higher grazing intensities. At higher shoot biomass levels an increase in shoots had little or no impact on total photosynthesis because photosynthetic rate per unit leaf area decreased. Total photosynthesis was maximized at lower shoot biomass levels in shorter grasses. Photosynthetic rates of grazed plants were stimulated by grazing. Light and water limitations on photosynthesis were lessened as greater quantities of water and light were available to each unit of leaf area of grazed plants.

Shoot morphology affected the relationship between total photosynthesis and belowground productivity as grazing regimes were altered (Fig. 3). The tall-grass exhibited a non-linear response because more photosynthate was allocated to shoots at low levels of total photosynthesis. The tall-grass produced the lowest quantity of belowground growth with a given quantity of photosynthate because it diverted a greater fraction of photosynthate to fewer, taller, and more lignified shoots. Clipped mid- and tall-grasses had much less belowground growth per unit of photosynthate than corresponding unclipped plants, while clipping did not have this effect on the short-grass.

The effect of shoot morphology was tested with the model by interchanging shoot morphologies of short- and tall-grasses (Table 2). All parameters regulating shoot growth, including shoot number, type, and size, tissue types, and growth rates, were reversed while the remaining biotic and abiotic parameters were held constant. The shoot system of the short-grass had at least twice as many meristems; however, tall-grass maximum individual shoot growth rates were several times higher, and the shoots could grow roughly three to four times larger.

Placing a tall-grass shoot system on the short-grass decreased above- and belowground productivities in all grazed plants. Only aboveground production of ungrazed plants was in-

TABLE 2. Effect of reversing shoot morphology between short- and tall-grasses on above- and belowground production (g/m²).

| Grazing Experiment | Aboveground Production | | | Belowground Production | | |
|---|---|---|---|---|---|---|
| | Ungrazed | Moderate | Severe | Ungrazed | Moderate | Severe |
| Control | 35 | 116 | 97 | 140 | 112 | 62 |
| Short-grass with | | | | | | |
| tall-grass shoots | 46 | 84 | 24 | 118 | 94 | 7 |
| Control | 214 | 512 | 90 | 301 | 158 | 8 |
| Tall-grass with | | | | | | |
| short-grass shoots | 196 | 419 | 509 | 353 | 324 | 82 |

creased. The interchange was especially harmful to severely grazed plants. Aboveground production of the ungrazed tall-grass was depressed by the short-grass shoot morphology, but belowground production was increased because less photosynthate was required by the smaller shoots. (Of course, the experiment did not account for reduced light competitive ability of shorter shoots.) When severely grazed, the tall-grass with short shoots performed considerably better.

Because shorter grasses had greater densities of smaller tillers, defoliation at a given height removed proportionately less foliage, and foliage below the grazing height was more concentrated. Grazing stimulated tillering and converted sparse, tall canopies into shorter ones with denser concentrations of younger, high quality foliage in both the model and in reality (McNaughton, 1976, 1984).

Modeling has explicitly shown that grazing responses are the result of interactions between morphological traits and physiological processes, and that the traits, the processes, and the interactions are, conversely, affected by grazing.

ADAPTATIONS IN INDIVIDUALS,
POPULATIONS, SPECIES AND COMMUNITIES

The importance of plant form in grazing response has been demonstrated both through experimentation and modeling. Shorter grasses had greater densities of smaller tillers, so defoliation at a given height removed proportionately less foliage, and foliage below the grazing height was more concentrated. However, morphological shifts to grazing-resistant forms can occur within individuals, populations, or communities. Grazing stimulates tillering, and convertes a sparse, tall canopy into a shorter "grazing lawn" that has a denser concentration of younger, higher quality forage (McNaughton, 1984). Grazing lawns can

result from phenotypic plasticity. This was simulated by the model, and shown in controlled experimentation discussed above. Phenotypic responses to grazing are reversed when grazing ceases (Quinn & Miller, 1967).

Another type of grazing lawn can be induced through long-term repeated grazing. Prostrate or dwarfed growth forms, often with a high ratio of basal to culmed meristems, may exist as infrequent ecotypes in ungrazed polymorphic populations. Recurrent, localized grazing may then increase the predominance of grazing-resistant ecotypes in the local sub-populations (Stapledon, 1928; McNaughton, 1979b, 1984; Detling & Painter, 1983; Detling et al., 1985), and the population as a whole would then be a mosaic of genetic variability. Alternatively, somatic mutations during asexual reproduction may facilitate evolution of genets and mosaics of genetic variability (Whitam & Slobodchikoff, 1981). Thus, a third type of grazing lawn could be comprised of plants that are inherently shorter, but also phenotypically plastic (McNaughton, 1984).

Finally, by reducing leaf area, opening up the canopy, creating small disturbance sites, and generally reducing the survival of grazing-intolerant species, grazing may alter competitive relationships in plant communities (Watkin & Clements, 1978; Edroma, 1981). In a grazed plant community lateral resource investment is more important, and shorter species may be favored where taller species would otherwise be competitively superior.

Thus, it is necessary to distinguish the impacts of grazing on individual plants from impacts on localized shifts in the distribution of ecotypes in a population, or species in a community. Since phenotypic plasticity is heritable (Bradshaw, 1974) and since polymorphism can be induced through disruptive selection, either could include examples of true grazing adaptiveness. However,

one must show that the grazing-resistant forms of plastic individuals are usually or only induced by grazing, that polymorphisms with grazing-resistant ecotypes only occur where there is, or was, periodic grazing, or that grazing ecotypes comprise more heavily grazed patches of a mosaic. In the case of non-plastic individuals or non-polymorphic populations, a trait can clearly be attributed to grazing selection pressure only if it is always more predominant, or if it only exists in reproductively isolated populations that are, or were, regularly grazed.

## Conclusions

Grasses and large grazing herbivores evolved together. However, it is difficult to show which graminoid traits arose or are solely maintained by grazing. Part of the difficulty, of course, is that we are unable to determine from the fossil record the precise origin of graminoid traits in relation to herbivore evolution. Extant grasses do withstand, avoid, or deter grazing, yet this does not constitute sufficient evidence for the selection of traits through coevolution with herbivores. I have given a number of examples of possible exaptations, or traits that could have arisen through non-herbivorous selection pressures, but which nevertheless confer benefits to grazed plants.

Either adaptive or exaptive traits may be more frequent among grazed (or ungrazed in the case of deterrence or avoidance) populations or species. If such a trait originally arose through non-herbivorous selection, but is now maintained in the gene pool of a population by grazing, or becomes more apparent in patches of grazed plants through differential survival, the trait should be considered truly adaptive. Similarly, phenotypic plasticity that is maintained by grazing is adaptive irrespective of original selection pressure.

Grasses differ markedly from dicotyledons in their lack of chemical defenses against herbivory. High concentrations of lignin and silica deter herbivory of grasses, but their primary functions are probably structural support and drought resistance. Ruminant microorganisms may make chemical defenses ineffective, and the array of other non-chemical means of coping with or avoiding herbivory may make chemical defenses unnecessary or non-cost-effective.

It is well worth speculation, in view of the novelty and potential importance of the concept, to admit that moderate grazing could have positive long-term effects on grasses (Owen & Wiegert, 1983). Perennial grasses persist for hundreds of years by vegetative reproduction, and moderate grazing can increase vegetative reproduction (McNaughton, 1983a). Thus, grazing can stimulate fitness. If so, natural selection would tend to encourage moderate herbivory of grasses. The lack of chemical deterrents and the high degree of adaptation or exaptation to herbivory among grasses support this possibility.

Experiments and simulation analyses showed that graminoid grazing responses are embedded in a context of interacting physiological processes and morphometric traits. Available water in the native habitat largely determines maximal stature and growth rate. In more mesic environments light competition and thus vertical growth are more important, leading to taller stature and less frequent optimal defoliation regimes. These constraints on plant form and function comprise an aptational context for graminoid responses to herbivory. Conversely, herbivory affects the responses of grasses to their abiotic environment. Therefore, it is necessary to explain defoliation responses in a systems context when referring to adaptive value.

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